Survival and Production in Variable Resource Environments

ERIK B. MULLER* AND ROGER M. NISBET
Department of Ecology,
Evolution and Marine Biology,
University of California,
Santa Barbara,
CA 93106-9610, U.S.A.
E-mail: muller@lifesci.ucsb.edu

A dynamic energy budget (DEB) model describes the rates at which organisms assimilate and utilize energy from food for maintenance, growth, reproduction and development. We study the dynamic behavior of one particular DEB model, Kooijman's κ-rule model, whose key assumption is that somatic and reproductive tissues are competing for energy. We assume an environment in which the food density fluctuates either periodically or stochastically (pink noise). Both types of fluctuations stimulate growth; the magnitude of the (average) increase in size depends on both the strength and duration of the fluctuations. In a stochastic environment, the risk of mortality due to starvation increases with increasing fluctuation intensity. The mean lifespan is also a function of the model parameter κ characterizing the partitioning of energy between somatic and reproductive tissues. Organisms committing a large fraction of resources to reproduction endure periods of food shortage relatively well. The effects of food fluctuations on reproduction are complex. With stochastic food, reproduction in survivors increases with increasing fluctuation intensities, but lifetime reproduction decreases. Periodic fluctuations may enhance reproduction, depending on the value of κ. Thus, a variable food supply stimulates growth, increases mortality and may enhance reproduction, depending on life history.

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INTRODUCTION

Organisms acquire energy from their environment and use it for growth and propagation. These and other expenditures are commonly modeled in terms of budgets. The simplest models assume a few fluxes that do not change over time, and use a mass or energy balance equation to analyse experimental results. More complex models use dynamic equations to describe the change of a potentially large number of many different budgets and fluxes. Models of both types abound in biology, and some date back more than a century (Duclaux, 1898). Our interest here is in simple

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*Author to whom correspondence should be addressed

dynamic models with a limited number of budgets, which we call dynamic energy budget (DEB) models. A DEB model describes the rates at which organisms assimilate and utilize energy from food for maintenance, growth, reproduction and development. These rates depend on the state of the organism (age, size, sex, nutritional status, etc.) and the state of its environment (food density, temperature, etc.). In this paper we study the behavior of one particular DEB model in a variable food environment.

Most DEB models are specific to one life stage of an organism or a (group of) species, the goal being to get a close match between data and model descriptions [see e.g., Kitchell *et al.* (1977), McCauley *et al.* (1990) and Mangel (1996)]. Another approach, followed here, is to use a single model that is sparse in parameters and mechanistically justifiable, but that nevertheless describes a broad spectrum of biological phenomena and life forms. Species are similar because they follow the same principles for budgeting, but they are different because they have different parameter values. A well-known example of this approach is von Bertalanffy's (1957) theory of growth, which uses only two parameters to fit the growth of many species with remarkable success. We study the most comprehensive model based on this approach, the κ-rule model developed by Kooijman (1986, 2000) (see Fig. 1). This model uses mechanistic reasoning to describe the growth and propagation of a wide range of species, ranging from bacteria to mammals, and with further mechanistic assumptions, the model can be used to derive inter-specific scaling relationships for physiological processes and body size. The model has been used in the study of the dynamics of (structured) populations (De Roos, 1997; Kooijman *et al.*, 1999), simple food chains (Kooi and Kooijman, 1994) and ecosystems (Kooijman and Nisbet, in press), and it provides a basis for many concepts used in ecotoxicology (Kooijman and Bedaux, 1996a,b).

Although DEB models, including the κ-rule model, were developed specifically for variable food environments (McCauley *et al.*, 1990; Ross and Nisbet, 1990; Kooijman, 2000; Lika and Nisbet, in press), to date most applications make an assumption of constant food. However, a model that fits organisms in a constant environment may not be appropriate when ambient conditions change with time. With constant food, different models can make similar predictions, whereas transient dynamics reveal the more distinctive implications of the assumptions of a model (Nisbet *et al.*, 1996). It is therefore important to analyse model behavior in a dynamic food environment.

We study the behavior of the κ-rule model in a fluctuating food environment. We consider two types of food fluctuations. One is a periodically variable food environment, which may represent diurnal or seasonal changes; the other is an environment in which food fluctuates stochastically but with some memory for previous food levels (pink noise). We study survival and performance as a function of the strength and the time scale of the food fluctuations, and also as a function of a potentially adaptive model parameter, the parameter specifying the division of resources between somatic and reproductive tissues. We first examine the dy-
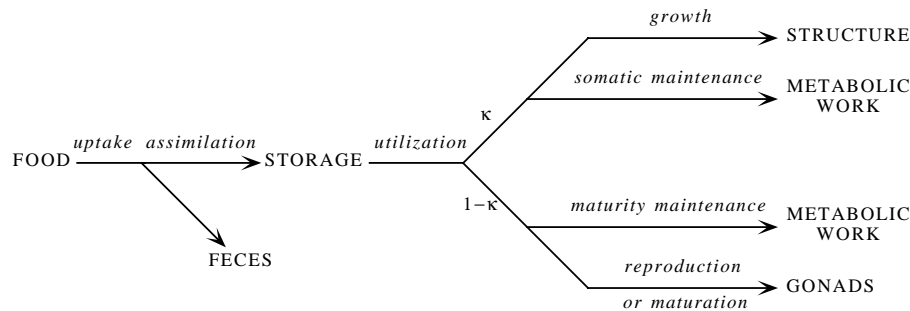
Figure 1. Kooijman's κ-rule model assumes that an organism ingests food at a rate dependent on its size and the food density (Kooijman, 2000). Energy is extracted from food and added to the reserves. The rate at which energy becomes available to the organism depends on its size and stored energy density. Provided somatic maintenance requirements are met, a fixed proportion κ of the available energy is allocated to somatic maintenance and growth combined, and the remaining $1 - \kappa$ to either maturation (for embryos and juveniles) or to reproduction and maturity maintenance (for adults). Growth ceases when this fixed fraction κ just meets somatic maintenance demands. Then, the organism may still reproduce, provided that energy made available exceeds the requirements for somatic and maturity maintenance.

namics of model equations analytically, which examination gives access to the long-term dynamics in a periodically fluctuating food environment. Because of the nonlinearities of the model, however, we need to rely on numerical studies for an understanding of the transient dynamics. Numerical analysis is also the primary means by which we study model behavior in a stochastically variable food environment. We illustrate model behavior with the marine mussel *Mytilus edulis*, for which realistic parameter values are available.

THE MODEL

The DEB model used in this study, the κ-rule model, is outlined in Fig. 1, and its assumptions are listed in Table 2. Kooijman (2000) has documented an elaborate justification of the assumptions, and a derivation of model equations can be found in Kooijman (1986, 2000), Zonneveld and Kooijman (1989), Van Haren and Kooijman (1993) and Nisbet *et al*. (1996). Here, for brevity, we restrict our presention of the model to ectothermic, heterotrophic organisms that do not change shape during growth [for a model extension that includes autotrophs see Kooijman and Nisbet (in press) and Kooijman (2000, pp. 159–185); for species that do change shape during growth, see, Kooijman (2000, pp. 26–29); and for endothermic organisms see, Kooijman (2000, pp. 92–96)].

The assumptions in Table 2 imply that the dynamics of an organism's growth and reproduction are described by two differential equations. One specifies the dynamics of structural body volume V, the other specifies the dynamics of the density of

Table 1. Symbols. A bar over a symbol refers to asymptotic values.

Symbol	Dimension	Interpretation
a	—	amplitude of scaled food density
a_c	—	critical amplitude of scaled food density
e	—	scaled stored energy density
$\bar{e}_c$	—	critical highest scaled stored energy density in limit cycle
$\bar{e}_{\max}$	—	highest scaled stored energy density in limit cycle
e_{rm}	—	scaled cumulative energy density committed to reproduction
f	—	scaled food density or scaled functional response
f_a	—	average scaled food density
g	—	energy investment ratio, $\propto \frac{1}{\kappa}$
L	length	shell length
m	time^{-1}	maintenance rate coefficient
r	time^{-1}	von Bertalanffy growth rate, $\frac{mg}{3(f+g)}$
S	time^{-1}	squared food fluctuation intensity
V	volume	structural biovolume
V_b	volume	structural biovolume at birth
V_m	volume	maximum structural biovolume, $\frac{\upsilon}{mg}$
V_p	volume	structural biovolume at maturation
V_∞	volume	ultimate structural biovolume at constant food, $f^3 V_m$
z	—	random variable
γ	time$^{-1/2}$	Gaussian white noise
κ	—	energy partitioning coefficient
τ	time	memory retention time
υ	volume$^{1/3}$ time^{-1}	energy conductance rate
ω	rad time^{-1}	angular frequency
ω_c	rad time^{-1}	critical angular frequency

the energy reserves, $[E]$, defined as the amount of stored energy per unit of structural volume. Reserve density has a maximum value $[E_m]$, which is independent of the size of the organism and the feeding conditions. The rate of change of stored energy density depends on the rate A at which energy is assimilated from food, and the rate at which energy is utilized. The assimilation rate is written in the form $A = A_m f V^{2/3}$, where the proportionality constant A_m represents the maximum surface area specific assimilation rate and f is the scaled functional response (type II). The rate at which energy reserves are released for utilization is a first order process inversely proportional to $V^{1/3}$. When maintenance requirements can be met this way, a fraction κ of the energy released from the reserves is used for the somatic processes of maintenance and growth, with maintenance having priority; the remainder is used for reproduction (adults), development (juveniles) and for maintenance of the state of maturity. This is the κ-rule. The κ-rule cancels when maintenance demands cannot be met this way. Then, maintenance requirements are being paid first, and the remainder is used for reproduction and development. When even this is insufficient, that is, the rate at which energy is released from

Table 2. Assumptions of the κ-rule model for ectothermic heterotrophs.

- There are two state variables: structural body volume, and stored energy density scaled to its maximum.
- There are six energy fluxes: assimilation; somatic maintenance; somatic growth; development; maintenance of the state of maturity; and reproduction. These energy fluxes are irreversible.
- There are maximally three life stages: embryos, which neither feed nor reproduce; juveniles, which may feed but do not reproduce; and adults, which may feed and reproduce.
- The rate of food uptake is proportional to the surface area of an organism, and is a hyperbolic function of the food density (type II functional response).
- Energy assimilated from food becomes part of the reserves. The dynamics of the energy reserve density are first order, with a rate that is inversely proportional to the volumetric length of an organism.
- A fixed fraction of the energy released from the reserves is commited to somatic maintenance and growth; the remainder is used for maturity maintenance, and development or reproduction. Maintenance demands have priority, and the partitioning of energy is modified to meet somatic maintenance.
- Death due to starvation occurs when somatic maintenance requirements cannot be met.
- The chemical compositions of structure and reserves are constant (homeostasis), and thus the following are constant:
    – the conversion efficiency of food into energy;
    – the cost to form a unit of structure;
    – the cost to maintain a unit of structure for a period;
    – the cost to maintain the state of maturity for a period;
    – the cost to form a unit of reproductive matter.
- Life stage transitions occur when the cummulative amount of energy spent on maturation exceeds a threshhold. An embryo initially has a negligibly amount of structure, and, when propagation is via eggs, its energy reserve density at hatching equals that of its mother during egg formation.

reserves is less than the rate at which energy is needed to maintain viability, the organism dies. It takes a constant amount of energy $[M]$ to maintain a unit of structure for a period of time, and a constant amount of energy $[G]$ to form a unit of structure.

Although the model describes flows of energy, our primary interest is in the dynamics of quantities (e.g., size, rate of reproduction) whose dimensions do not involve energy. It is convenient to scale variables and parameters to take account of this, and, following Kooijman (2000), we define the following quantities: the scaled density of energy reserves, $e \equiv \frac{[E]}{[E_m]}$; the energy conductance rate, $\upsilon \equiv \frac{A_m}{[E_m]}$; the maintenance rate coefficient, $m \equiv \frac{[M]}{[G]}$; and the investment ratio, $g \equiv \frac{[G]}{\kappa[E_m]}$. Note that g depends on κ, a primary parameter we use explicitly at several points in this study. This scaling with g is a bit unfortunate, but is a price worth paying to retain notation consistent with the large body of literature on the κ-rule model.

With e replacing $[E]$ as the state variable for energy reserves, the state equations now become

$$\frac{de}{dt} = \upsilon V^{-\frac{1}{3}}(t)(f(t) - e(t)), \tag{1}$$

$$\frac{dV}{dt} = \frac{(ve(t)V^{\frac{2}{3}}(t) - mgV(t))_+}{e(t) + g}, \tag{2}$$

The subscript '+' in equation (2) means that an organism cannot shrink, i.e., $\frac{dV}{dt} = 0$ whenever $ve(t)V^{\frac{2}{3}}(t) - mgV(t) < 0$, i.e., when the default energy committed to somatic tissues is insufficient to meet maintenance demands. The maximum structural body volume, V_m, an organism can attain is $V_m = \left(\frac{v}{mg}\right)^3$; V_m is proportional to κ^3, because of its dependency on g.

We also seek to quantify reproduction. The assumptions specify the rate at which energy is committed to reproduction. We divide the amount of energy committed to reproduction by the maximum structural volume an organism would attain with abundant food if it were to devote all its energy to somatic tissues, and scale the resulting density by the maximum possible density of the energy reserves. This measure is the scaled cumulative reproductive output, e_{rm}. Provided that the organism has reached the size of an adult, that is $V \geq V_p$, the dynamics of e_{rm} follow (Kooijman, 2000, pp. 100–101)

$$\frac{de_{rm}}{dt} = \begin{cases} \frac{\kappa^3(1-\kappa)}{V_m}\left(\frac{ge(vV^{2/3}+mV)}{g+e} - mgV_p\right) & \text{if } e \geq \frac{V^{1/3}}{V_m^{1/3}} \\ \frac{\kappa^3}{V_m}(veV^{2/3} - mg(\kappa V + (1-\kappa)V_p))_+ & \text{if } \frac{\kappa V^{1/3}}{V_m^{1/3}} > e > \frac{V^{1/3}}{V_m^{1/3}}. \end{cases} \tag{3}$$

The first condition is true for growing organisms, whereas the second applies to non-growing individuals. Note that this equation does not necessarily define the actual reproduction rate. The model assumes a continuous and irreversible allocation of energy reserves for reproductive purposes, but the release of reproductive matter may be a discrete event.

The model simplifies considerably when the food level is constant. The scaled density of stored energy will approach an equilibrium, that is, $\bar{e} = f$, so that equation (2) can be solved analytically. The solution of equation (2) is the well-known von Bertalanffy growth equation,

$$V^{1/3}(t) = V_\infty^{1/3} - (V_\infty^{1/3} - V_0^{1/3})e^{-rt}, \tag{4}$$

where $V_\infty^{1/3} = fV_m^{1/3}$ is the ultimate volumetric length of the organism at a given food level, and $r \equiv \frac{mg}{3(f+g)}$, is the von Bertalanffy growth rate parameter which defines how fast an organism approaches its ultimate size. For practical purposes, the volumetric lengths in equation (4) can be substituted for an experimentally convenient length measure, such as shell length in mussels, since we confined this presentation to isomorphic organisms.

FOOD AVAILABILITY

We now want to understand how model organisms perform in a variable food environment. Food levels may fluctuate in many different ways. We consider two

idealized forms of variation, one in which food levels vary deterministically, and one in which food levels are in part driven by a stochastic process. For both types, we assume that the variations operate directly on the scaled functional response rather than on the food density, an assumption that makes it relatively easy to compare model behavior under different fluctuation regimes. The form of the scaled functional response in the model is type II, but we note that our analysis holds for any dimensionless form that takes values between 0 and 1.

For deterministic food variations we assume a periodically changing food environment resembling, for instance, the alternation of high and low food due to diurnal or seasonal changes. For simplicity, we only consider single frequency variations. Assuming a scaled functional response that fluctuates sinusoidically with an amplitude a, angular frequency ω, and a mean value f_a between 0 and 1, we have

$$f(t) = f_a + a \sin(\omega t), \qquad a \leq \min\{f_a, 1 - f_a\}. \tag{5}$$

Over a full period, the mean scaled functional response is f_a, and the mean square deviation from f_a is $0.5a^2$. In contrast to the symmetrical fluctuations in the scaled functional response, the unscaled food density shows narrow seasonal peaks and changes little in the off-season, a pattern that gets more pronounced with increasing f_a and a. This pattern is consistent with food variations in environments in which a season with excess food alternates with a longer, less productive season, a pattern common in temperate and polar regions.

In order to simulate a stochastic environment, we assume pink noise $z(t)$ is added to the mean value for the scaled functional response [see, Nisbet and Gurney (1982, pp. 240–246)]. However, because $0 \leq f \leq 1$, we require to bound possible outcomes to ensure f stays within this range. So,

$$f(t) = \begin{cases} 0 & \text{if } f_a + z(t) < 0 \\ f_a + z(t) & \text{if } 0 \leq f_a + z(t) \leq 1 \\ 1 & \text{if } f_a + z(t) > 1, \end{cases} \tag{6}$$

where $z(t)$ is a random variable whose dynamics are given by

$$\frac{dz}{dt} = \frac{-z}{\tau} + S^{1/2}\gamma(t), \tag{7}$$

in which τ is the memory retention time, which quantifies the exponentially fading memory for previous values of $z(t)$, and γ is Gaussian white noise with intensity $S^{1/2}$. The pink noise assumption ensures that food is likely to be abundant at some time if it was abundant just prior to that moment, and scarce when it was scarce just before. Gaussian white noise generates a random walk, but f is bounded here. Unless $f_a = 0.5$, the distribution of $f(t)$ is skewed, and this skewedness increases with the intensity of the fluctuations. When $f_a = 0.5$ the distribution is symmetrical. Then, like the deterministic case, the expected value for the scaled functional response is f_a and, while depending on the cut off of f, the mean square displacement from f_a is maximally $S^2\tau$.

Dynamics in Variable Food Environments

We wish to solve two questions with regard to variable food environments. First: 'Can an organism survive in a variable food environment?', and second: 'Given that an organism survives in a variable food environment, what is the form of the long-term dynamics?' The latter question is relevant since older organisms that have (apparently) ceased growth will have dynamics that are arbitrarily close to those long-term dynamics. Because of the nonlinearities in the model, neither the transient dynamics with deterministically fluctuating food, nor the behavior of the model when food varies stochastically can be determined analytically. In a later section, we address these issues via numerical studies. We show here that, under certain circumstances, an organism may survive a periodically varying food environment for an indefinite time, and that the long-term dynamics of the state variables determine the environmental conditions for survival at any time. We also compare long-term reproduction in periodically variable food environments with that in a constant environment.

We show in the Appendix that, provided the organism survives, its scaled energy reserve density approaches the limit cycle

$$\bar{e}(t) = f_a + \frac{a}{\sqrt{1 + \left(\frac{\omega \bar{V}^{1/3}}{\upsilon}\right)^2}} \sin(\omega t + \phi), \tag{8}$$

where $\phi = \tan^{-1} \frac{\omega \bar{V}^{1/3}}{\upsilon}$, is a measure (in radians) of the extent to which fluctuations in e ultimately lag behind f. The organism continues to grow until it attains a size $\bar{V}$ given by

$$\bar{V} = \left(\frac{\bar{e}_{\max} \upsilon}{mg}\right)^3, \tag{9}$$

with $\bar{e}_{\max}$ being the highest scaled energy density in the limit cycle, which occurs when $\sin(\omega t + \phi) = 1$. Figure 2 illustrates the transient approach to the long-term dynamics discussed above.

Equations (8) and (9) reveal three important model features. First, the long-term dynamics of e and V are independent of initial conditions. Provided an organism can survive periods of low food availability, it will ultimately grow to a certain size and exhibit certain reserve dynamics independent of the season it was born. Second, the highest scaled energy density in the limit cycle and the ultimate size increase with the amplitude of the food fluctuations. Thus, surviving organisms grow bigger the more intense the fluctuations in the food environment. Third, the capacity of the energy reserves to buffer changes in the food environment depends on the rate at which the food environment changes relative to the dynamics of energy reserves. When food levels are changing relatively slowly, that is ω is small, $\bar{e}_{\max}$ will be close to $f_a + a$, and reserves are fluctuating with an amplitude similar
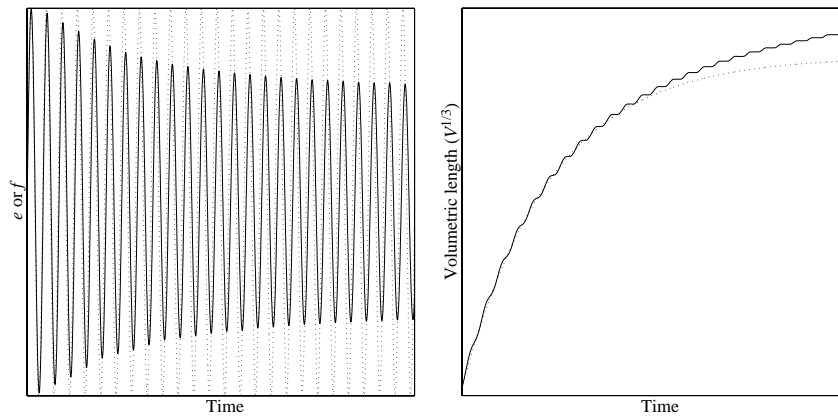
Figure 2. The scaled stored energy density (solid curve; left curve) tracks (with a lag) the scaled food density (dotted curve; left panel) in a variable food environment. As the organism grows, the time that the scaled stored energy density lags behind the scaled food density increases, while the amplitude of the energy density decreases. Its length as a function of time is shown in the right panel (solid curve); the dotted curve in the right panel represents growth at constant food.

to that of food availability. However, in a rapidly changing food environment $\bar{e}_{\max}$ will be close to f_a and, from the organism's point of view, the environment will be virtually constant.

Now assume that an organism is born into an environment similar to that of its mother, implying that $e(0)$ is in the range of values for the scaled functional response it will experience (see Table 2). Then, if an organism is able to survive through a limit cycle, it is also able to survive through the transient (see the Appendix). Thus we can simply study long-term dynamics in order to answer questions about the environmental conditions that ensure viability. The organism grows to a size proportional to the highest scaled energy density in the limit cycle, but its long-term survival depends on the lowest scaled density of energy reserves in the limit cycle $\bar{e}_{\min}$. Equation (8) implies $\bar{e}_{\min} = \bar{e}_{\max} - 2a\left(1 + \left(\frac{\omega \bar{e}_{\max}}{mg}\right)^2\right)^{1/2}$. Because survival requires that $V(t) \leq \left(\frac{e(t)v}{\kappa mg}\right)^3$ for all t (see the Appendix), we get the following condition for long-term survival:

$$\frac{2a}{\sqrt{1 + \frac{\omega^2 \bar{e}_{\max}^2}{m^2 g^2}}} - \bar{e}_{\max}(1 - \kappa) \leq 0. \tag{10}$$

Using equations (8)–(10), we can now determine the highest scaled density $\bar{e}_c$ of energy reserves in an organism that is just able to survive,

$$\bar{e}_c = \frac{2f_a}{1 + \kappa}. \tag{11}$$

The highest amplitude a_c at which an organism is able to survive periods of low

food is

$$a_c = (\bar{e}_c - f_a)\sqrt{1 + \frac{\omega^2 \bar{e}_c^2}{m^2 g^2}}, \qquad (12)$$

which reduces to

$$a_c = f_a \frac{1 - \kappa}{1 + \kappa} \qquad (13)$$

in a very slowly changing food environment. Finally, the slowest angular frequency ensuring survival from starvation is ω_c, with

$$\omega_c = \frac{mg(1 + \kappa)}{2f_a}\sqrt{\left(\frac{a(1 + \kappa)}{f_a(1 - \kappa)}\right)^2 - 1}. \qquad (14)$$

A prominent role in these expressions for critical values is played by κ, the parameter that defines the partitioning of resources over somatic and reproductive tissues (note that the compound parameter g is inversely proportional to κ). Indirectly, it also determines the organism's abilities for surviving poor food conditions; the potential for survival declines with decreasing κ.

Having determined the long term behavior of the state variables, we can now calculate long-term reproduction. From equation (3) the long-term reproduction rate is

$$\frac{d\bar{e}_{rm}}{dt} = \kappa^3 mg\left(\bar{e}_{max}^2 \bar{e}(t) - \kappa \bar{e}_{max}^3 - (1 - \kappa)\frac{V_p}{V_m}\right), \qquad (15)$$

with $\bar{e}(t)$ given by equation (8). Integration over a full period then yields the ultimate reproductive output in one cycle ρ, as

$$\rho = \frac{2\pi}{\omega}\kappa^3 mg\left(\bar{e}_{max}^2 f_a - \bar{e}_{max}^3 \kappa - (1 - \kappa)\frac{V_p}{V_m}\right). \qquad (16)$$

Unlike long-term growth, ultimate reproduction may be reduced in a variable food environment. In a constant environment the ultimate reproduction during a time interval $2\pi/\omega$ equals

$$\frac{2\pi}{\omega}\kappa^3 mg(1 - \kappa)(f_a^3 - V_p/V_m). \qquad (17)$$

Thus, ultimate reproduction in a constant environment exceeds that in a variable food environment when $\kappa \geq \frac{\bar{e}_{max}^2 f_a - f_a^3}{\bar{e}_{max}^3 - f_a^3}$. Organisms with $\kappa \in \left(0, \frac{\bar{e}_{max}^2 f_a - f_a^3}{\bar{e}_{max}^3 - f_a^3}\right)$ perform better in a variable food environment.

Table 3. Parameter values of the mussel *Mytilus edulis* with $\kappa = 0.8$.

Symbol	Value	Correction factor[a]	Reference
d_m[b]	0.333	—	(Van Haren and Kooijman, 1993)
g	1.286	$\frac{0.8}{\kappa}$	(Van Haren and Kooijman, 1993)
L_b	0.001 m	—	(Seed, 1976)
L_m	0.100 m	$\frac{\kappa}{0.8}$	(Van Haren and Kooijman, 1993)
L_p[c]	0.003 m	$\frac{\kappa}{4(1-\kappa)}$	(Seed, 1976)
m[d]	0.583 y^{-1}	—	(Kooijman, 2000, p. 275)
υ[d]	0.075 m y^{-1}	—	(Kooijman, 2000, p. 275)

[a] The values of parameters that depend on κ are calculated by multiplying the correction factor with the value listed. [b] Converts volumetric length into shell length, $L = d_m V^{1/3}$. [c] The assumptions imply $L_p \propto \kappa/(1 - \kappa)$ (Zonneveld and Kooijman, 1989). [d] Normalized to 20 °C (Kooijman, 2000).

NUMERICAL STUDIES

In the previous sections, we analysed the behavior of the κ-rule model in a dynamic food environment. We were able to specify long-term dynamics and survival conditions in the situation where food varied deterministically. However, transient dynamics with deterministic food remained largely undetermined, as did the behavior of an organism in a stochastic environment. In the next two subsections, we study our system numerically. We explore model behavior as a function of environmental parameters in the forcing functions, and as a function of the life history parameter κ, since this parameter tends to be highly variable within a species. We illustrate model behavior with parameters appropriate for the marine mussel *Mytilus edulis* (see Table 3); initial values not mentioned in the table are $f(0) = 0.5$ and $e(0) = 0.5$, and the phase of the period with deterministic food fluctuations is 0 rad.

We assume an environment in which food levels vary either deterministically or stochastically around $f_a = 0.5$, which allows us to explore a maximum range of fluctuation intensities. We wish to be able to compare in some systematic way the results of the deterministic and stochastic simulations, and therefore calibrate the stochastic intensity of food fluctuations, $S^{1/2}$, to the deterministic amplitude a. We set $S = a^2/\tau$, so that, neglecting the effects of cut off of f in the stochastic case, the mean squared displacement of f from f_a is similar with both types of food variation. With periodically variable food, we consider fluctuations with a period of a day, year and decade, which, relative to a mussel's physiology, represent a food density that is changing rapidly, moderately slowly or very slowly. For stochastic food, we take the memory retention time τ in stochastic simulations equal to the period of the deterministic cycles, since this yields sets of deterministic and stochastic runs in which the memory for previous food values operate on a similar time scale. In addition, we study the effects of a really long retention time, corresponding to a period of a century in our transformation, which may serve

as a caricature of climatologically induced changes in food availability beyond an organism's life span.

1. PERIODIC FOOD

We now analyse dynamics in a periodically variable food environment, and study how the performance of mussels changes with the amplitude, and period of the fluctuations, as well as with κ, the partitioning coefficient of growth and reproduction. Only two of the three periods studied, a year and a decade, have a significant effect on the performance of mussels. Daily fluctuations are so fast that from the mussel's point of view the environment is essentially stable. Regardless of the intensity of the fluctuations, the scaled stored energy density e fluctuates minimally, and consequently, growth and reproductive output with daily food fluctuations are indistinguishable from production at the average, constant food level (results not shown). Furthermore, daily fluctuations do not impair the mussel's ability to survive. Equation (14) gives the period of fluctuation critical for long term survival. With $f_a = 0.5$, a mussel with $\kappa = 0.9$ can withstand any fluctuation with a fluctuation less than 12 days; a mussel with $\kappa = 0.1$ can survive fluctuations with a period less than 2 months.

Fluctuations with periods of a year or a decade do have a significant impact. We demonstrated above that the ultimate length is proportional to the maximum stored energy density in the limit cycle [see equation (9)]. In line with this, Fig. 3 shows that mussels with variable food are almost always bigger than their conspecifics at constant food. With an annual fluctuation [see Fig. 3(a)], the exceptions are found in the bad periods during the early years (this trend is most pronounced when the phase is a half period—simulations not shown). Also, the time to reach a size arbirarily close to the ultimate size increases with amplitude. The fraction of a period in which e is sufficiently high for growth declines in time, causing the growth trajectory to flatten off slowly, this trend being more pronounced at higher amplitudes. Qualitatively similar results are obtained with a period of a decade. Figure 3(b) and (c) show trends that are more pronounced than with annual fluctuations.

Organisms not only grow bigger when there are large fluctuations in the food environment, they also consume more food. A question of economic interest, e.g., in mariculture, is how the efficiency of biomass formation depends on fluctuations in food supply. We express this efficiency in terms of a cumulative yield, defined as the ratio of the amount of structure formed to the cumulative amount of food consumed, and scale this yield to the yield at constant food. There is a subtle problem involved in this measure: it ignores the reserves, which may, in part, become structure. Therefore, in comparisons with this cumulative yield measure, only individuals with an equal amount of stored energy should be considered. Scaled cumulative yields show two trends (results not shown). First, yields oscillate in
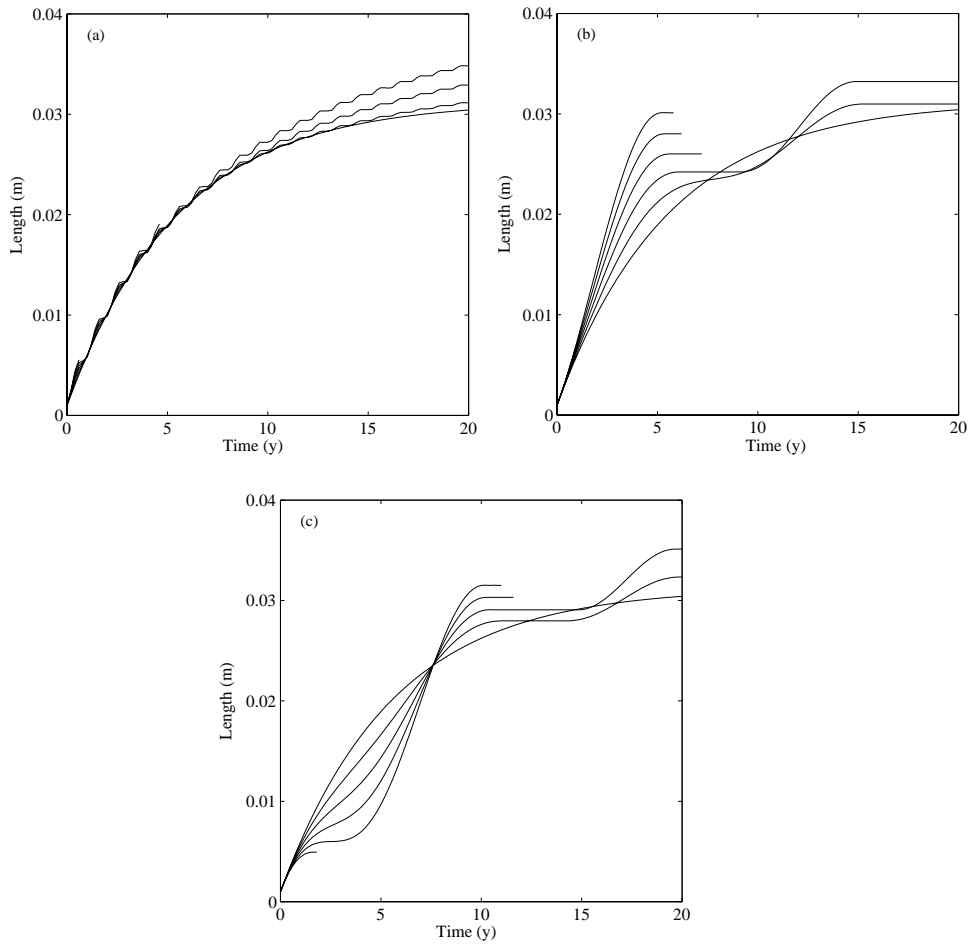
Figure 3. Periodic food fluctuations stimulate growth. The period of the fluctuations is (a) a year; (b) a decade with the simulations starting at the onset of the growth season; and (c) a decade with the simulations starting at the onset of the bad season. The smooth curve refers to growth at constant food ($f = 0.5$), and subsequent curves mark growth at increasing amplitudes [(a) ranges from 0.1 to 0.5 with 0.1 intervals]; growth curves end when the organism starved to death. Parameters values are for the mussel *Mytilus edulis* (see Table 3) with $\kappa = 0.5$.
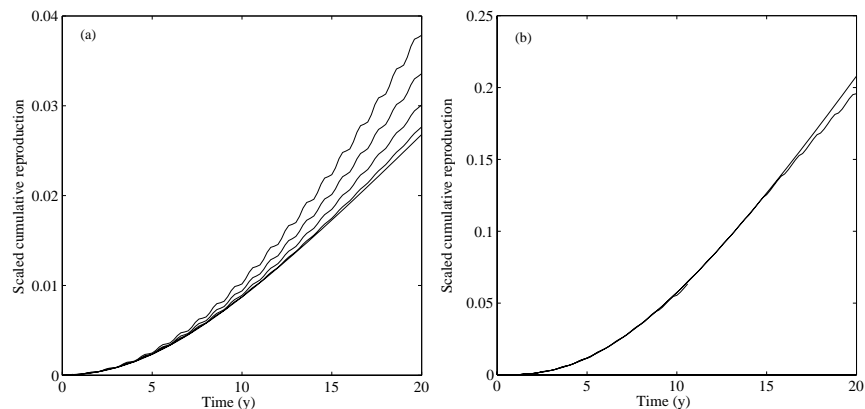
Figure 4.   Periodic food fluctuations enhance the reproductive output of organisms that already commit relatively a large fraction of their resources to reproduction [(a), $\kappa = 0.1$], but reduce reproduction in organisms favoring growth over reproduction; [(b), $\kappa = 0.9$]. The smooth curve refers to reproduction at constant food ($f = 0.5$), and subsequent curves mark growth at increasing amplitudes [(a) ranges from 0.1 to 0.5 with 0.1 intervals] in an annually fluctuating food environment; interrupted curves, some of them hardly distinguishable in the right panel, indicate that the organism starved to death. Parameters values are appropriate to the mussel *Mytilus edulis* (see Table 3).

response to fluctuations in food availability. Second, scaled cumulative yields are, initially, higher with increasing amplitude. Later this trend is reversed, but not until the organism has approached its ultimate size fairly closely. This implies that food fluctuations enhance the efficiency of biomass formation as long as there is substantial growth.

Perhaps more important from an ecological perspective is how food fluctuations affect reproductive output. As discussed in a previous section, food fluctuations enhance the long-term reproduction of surviving mussels that have a relatively low value for κ, whereas fluctuations decrease the reproductive output of mussels with a high value for κ. These trends emerge early, as Fig. 4(a) illustrates for a mussel with a low κ living in an environment with annually varying food. With a high κ, the trend is less conspicous since animals soon starve to death under those conditions [see Fig. 4(b)]. The figures also show that κ has a great effect on reproduction. Mussels with a high κ reproduce more than those of the same age with a low κ.

The life span of mussels may decrease dramatically when the availability of food fluctuates, especially when κ is high (see Fig. 5). κ specifies the partitioning of energy between somatic and reproductive tissues, and therefore determines the size to which a mussel will grow. Since larger animals require more energy for maintenance purposes, a higher value for κ may imply a reduction in life span. The amplitude of the food fluctuations determines the level to which the energy reserves will decline during the off season, and thus directly affects the survival potential of a mussel, but it also indirectly affects the life span of a mussel through its stimulating effects on growth. The period of the fluctuations is also important because the
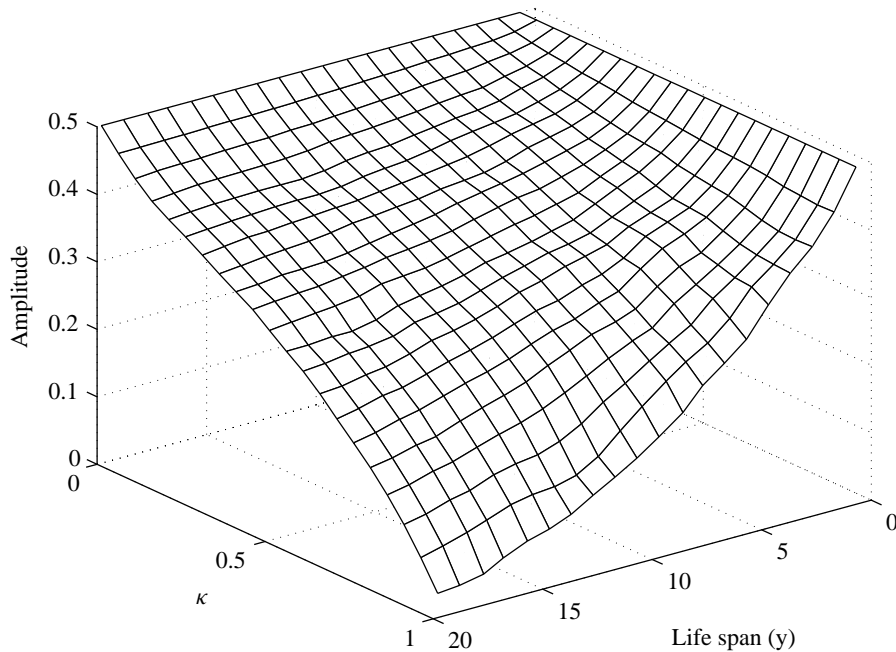
Figure 5. The life span of organisms is reduced by the amplitude of food fluctuations and by κ; a low value for κ implies an individual that commits a relatively large fraction of resources to reproduction and a small fraction to growth. Parameters values are appropriate to the mussel *Mytilus edulis* in an annually variable food environment (see Table 3).

buffering capacity of the storage compartment declines when the period increases. Finally, the timing of birth may be crucially important, as is illustrated by Fig. 3(b) and (c). These figures show simulations when the period of the fluctuations is ten years, which is such a long period that the dynamics of stored energy closely follow the dynamics of food. Mussels that started their settled life at the onset of the good period will survive for at least 5 years. They are born into an environment that initially becomes increasingly hospitable, and then grow to a large size, especially at high values for κ. They therefore quickly die when food becomes scarce. On the other hand, mussels that settle at the onset of the bad spell remain small, which, except at the highest amplitudes, enables them to survive until the next bad period. They thus become older than their conspecifics that start life with a feast.

2. STOCHASTIC FOOD

We again study the behavior of the model as a function of the partitioning coefficient κ and as a function of environmental variation, which in the case of stochastically fluctuating food is characterized by two parameters: the intensity of the food fluctuations and the memory retention time of previous food levels. We first illustrate model behavior with sample realizations of food and storage dynamics, and

then examine expected production and survival patterns (a 1000 realizations are used to calculate expected values).

Figure 6(a) and (c) show samples of environments in which food fluctuates with a moderate intensity and with a memory retention time of a day or a year. Figure 6(b) and (d) show corresponding dynamics of the scaled density of energy reserves in a mussel. Dynamics of energy reserves are smoother than those of food. Reserves buffer changes in the food environment, and changes with the highest frequency are the ones that are most effectively buffered. As a result, the mussel experiences an environment in which food fluctuates with a memory retention time of a day as it were relatively stable. With higher memory retention times, however, the scaled density of energy reserves follows relatively closely the scaled food density; with a memory retention time of a century, the trends of both densities are essentially the same (results not shown). Figure 6(a) and (b) also indicate that the buffering capacity is a function of size. The buffering capacity increases in time, since the mussel has grown over time (results not shown), resulting in slower storage dynamics [cf. equation (1)].

On average, the size and cumulative reproductive effort of mussels increase with the intensity of food fluctuations (see Fig. 7). Organisms in variable food environments tend to be bigger and to reproduce more than their conspecifics in a constant food environment. This increase is also a function of the memory retention time of the fluctuations in food supply. The increase in production with variable food is negligibly small when the memory retention time is a day (results not shown), but with a retention time of a year (results not shown) or a decade (see Fig. 7) the increase is substantial. With a memory retention time of a decade, at the highest fluctuation intensity examined, the average length after 20 years is about 40% percent higher and reproductive output is more than twice as high as production at constant food. However, with even higher memory retention times, this increase of production with fluctuation intensity becomes less pronounced. In an environment in which food fluctuates with a memory retention time of a century, the percentage of increase is 10% and 25% for length and cumulative reproduction, respectively (results not shown).

Thus, growth and reproduction are predicted to be highest in environments where food levels vary strongly but slowly. One reason for this is that high levels of food densities become more common at higher fluctuation intensities. This causes mussels to be fat for occasional periods, during which they commit extra energy to growth. Because organisms cannot shrink, they become bigger in a variable food environment, and larger organisms reproduce more. This mechanism for enhanced production is increasingly important with increasing memory retention times. With a low memory retention time, extremes in food densities do not last long and are thus effectively buffered by the energy reserves. With a high memory retention time, reserve levels track the availability of food, and extreme food levels translate into high reserve levels. When the memory retention time is substantially higher than the lifespan, however, the mussel experiences relatively little variation in food
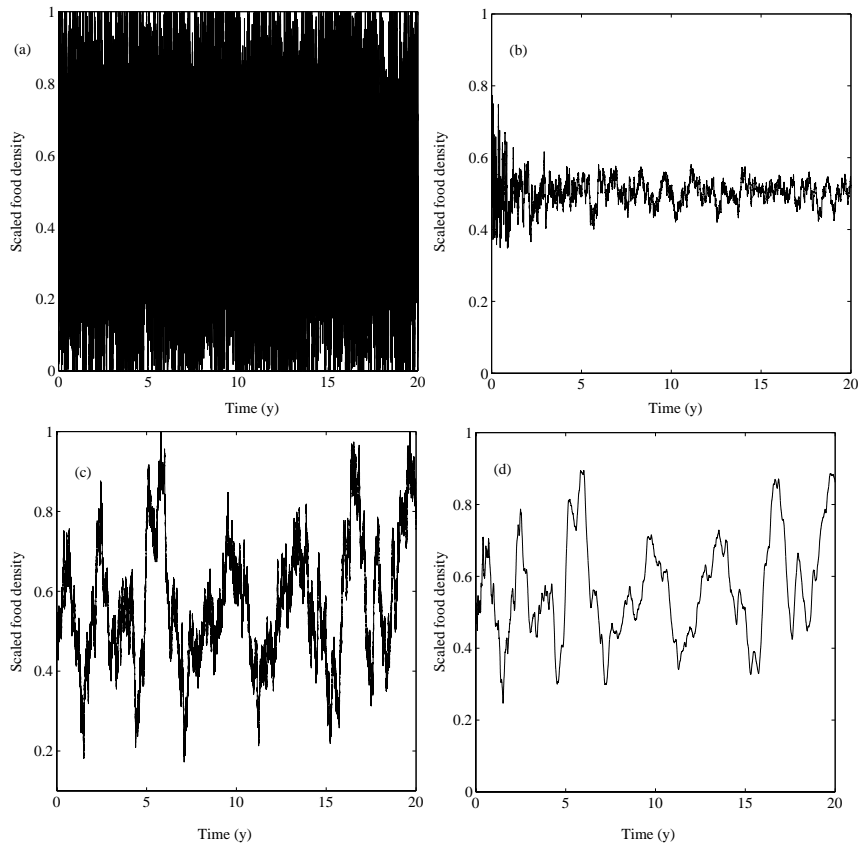
Figure 6. An organism experiences changes in its food environment through changes in its reserves. In a stochastic environment with a memory retention time of 1 day, the scaled food density (a) is much more volatile than the scaled stored energy density (b); with a memory retention time of 1 year, the scaled food density (c) is more closely followed by the scaled stored energy density (d). Parameters values are appropriate to the mussel *Mytilus edulis* (see Table 3) with $\kappa = 0.5$ and $S = 0.09\tau^{-1}$.
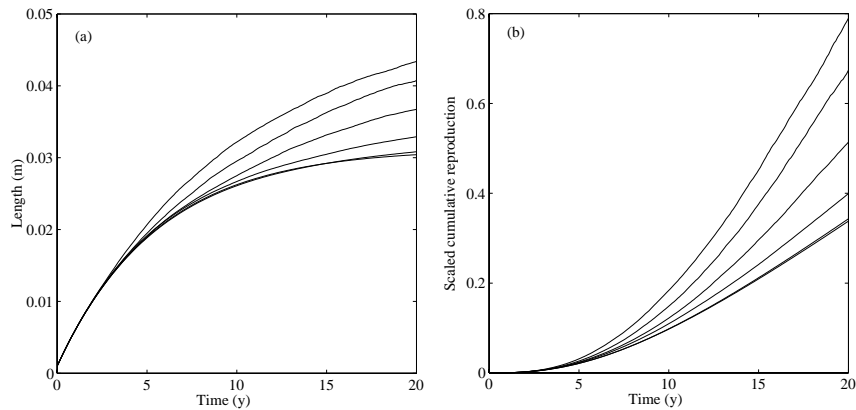
Figure 7. The average size (a) and reproduction (b) of surviving organisms increases with the intensity of stochastic food fluctuations. From top to bottom and in sequential order, the curves represent average production with $S = 0.025y^{-1}$, $0.016y^{-1}$, $0.009y^{-1}$, $0.004y^{-1}$, $0.001y^{-1}$ and $0y^{-1}$, respectively. Parameters values are appropriate to the mussel *Mytilus edulis* (see Table 3) with $\kappa = 0.5$ and $\tau = 10y$.

availability during its life time; production patterns are then relatively close to those observed at constant food conditions.

There is another mechanism explaining why average size and reproduction increase with the intensity and memory retention time of food fluctuations. When the value of these two parameters increase, the likelihood of persistently low levels of food and energy reserves, and thus starvation, increase as well. Survivors are likely to have experienced the relatively better food environments. Therefore, the scaled density of energy reserves in surviving mussels tends to increase with time. At the highest fluctuation intensity, the upward drift in reserve levels after 20 years ranges from zero with a retention time of a day to 40% with a memory retention time of a decade. Those elevated levels of energy availability evidently support higher levels of average growth and reproduction.

The probability of survival to any given age depends on the intensity and memory retention time of the food fluctuations (see Fig. 8). Survival probabilities decline when food fluctuations become more intense. The effect of the memory retention time on survival is more complex. The survival probability to any given age shows a minimum at some intermediate memory retention time. With a memory retention time of a day, death through starvation is a sporadic event, even at the highest fluctuation intensity (results not shown). At the highest intensity with a memory retention time of a year, however, none of the 1000 realizations included an organism that survived for 20 years [see Fig. 8(a)]. With higher memory retention times, the odds for survival improve [see Fig. 8(b)], and mortality is not an important issue when the memory retention stretches well beyond the life span of the organism [see Fig. 8(c)]. The reason for this is that the organism is then unlikely to experience large environmental change during its life time. We note that the
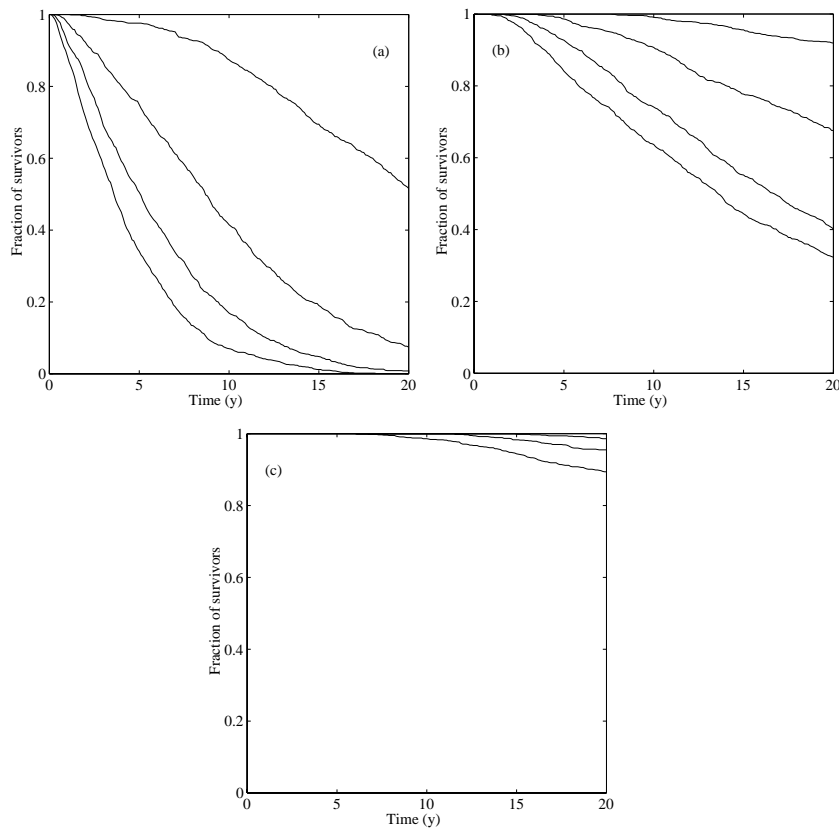
Figure 8.   The probability of survival to a given age in a stochastically variable food environment declines with the intensity of the food fluctuations and depends on the memory retention time of the environment for previous food levels. The memory retention time τ is (a) $1y$, (b) $10y$ or (c) $100y$ (with $\tau = 1d$, survival was 100%). In all panels, the curves represent survival probabilities with, from bottom to top and in sequential order, $S = 0.25\tau^{-1}$, $0.16\tau^{-1}$, $0.09\tau^{-1}$, $0.04\tau^{-1}$, respectively. With $S = 0.01\tau^{-1}$, mortality is nil. Parameters values are appropriate to the mussel *Mytilus edulis* (see Table 3) with $\kappa = 0.5$.

survival probability depends on κ, because organisms with a low value of κ remain relatively small and are better able to survive periods of starvation.

So far, we have discussed average cumulative production of organisms that managed to survive in a stochastically variable food environment, that is, the average cumulative production of survivors. The question remains how fluctuations in food availability affect the expected future cumulative production of a newborn. Calculations of those measures include the final size and cumulative reproduction output of dead mussels. At the lower fluctuation intensities, mortality remains of minor importance during the time spanned by the simulation, and thus the average production of survivors of a given age is close to the expected future cumulative production of a newborn once it has reached the same age (see Fig. 9). At the
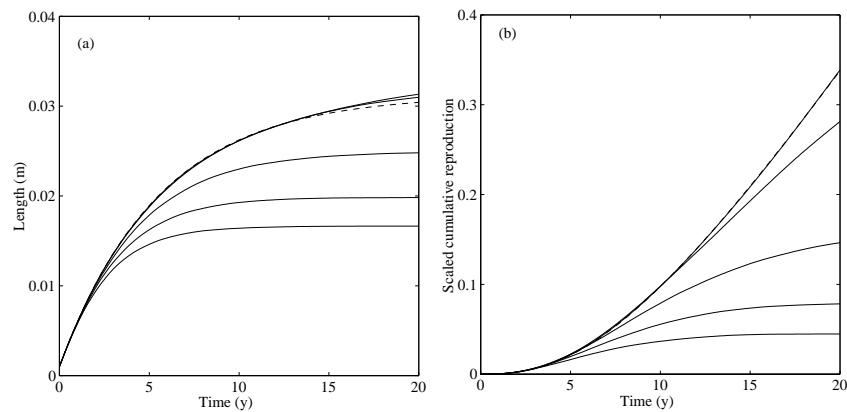
Figure 9. The expected growth (a) and reproduction (b) to a given age are stongly reduced by intense stochastic food fluctuations because of mortality due to starvation, but mild food fluctuations may stimulate production. The dotted curve in both panels represent production at constant food, and the solid curves represent production with, in sequential order and from bottom to top, $S = 0.25y^{-1}$, $0.16y^{-1}$, $0.09y^{-1}$, $0.04y^{-1}$ and $0.01y^{-1}$, respectively. Parameters values are appropriate to the mussel *Mytilus edulis* (see Table 3) with $\kappa = 0.5$ and $\tau = 1y$.

higher fluctuation intensities, however, the expected future cumulative production of a newborn tends to stabilize as time progresses, since the number of survivors declines (see Figs 8 and 9). Then, the expected future size of a newborn remains substantially smaller than with constant food, although the average size of surviving mussels increases with fluctuation intensities. Even more dramatic is the decline in the expected future cumulative reproduction of a newborn with increasing fluctuation intensities. Whereas individuals in a stable food environment keep producing off-spring at a steady rate, the expected future reproduction rate of a newborn declines in time in an intensely variable food environment (see Fig. 9) as mortality takes it toll. Then, the expected future cumulative reproductive output converges to lifetime production as the probability of survival to a given age approaches zero. Those trends of expected future reproduction and growth of newborns no longer hold with very long memory retention times. Mortality then has relatively little impact, even at the higher fluctuation densities.

DISCUSSION

The model makes the following predictions about (average) growth and mortality in a variable environment. Organisms grow bigger in a variable food environment than in a constant environment with similar average food availability. Ultimate size increases with the amplitude and period of deterministic food cycles, and with the intensity and memory retention time of stochastic food fluctuations. In variable food environments, organisms grow to a size related to the peaks in food availability, rather than to the mean. Food fluctuations may lead to death from starvation,

the likelihood of which increases with the strength and duration of the fluctuations. Two processes are involved here: starvation requires a sustained period of low food, but in addition the larger individuals that are present in a fluctuating environment have greater maintenance costs than their smaller counterparts living at constant food and are hence particularly vulnerable to food stress. These mechanisms of starvation are also in effect at the population level when organisms are able to deplete their food source (Kooijman *et al.*, 1989).

Model predictions on growth in periodic food environments are in line with observations backing Bergmann's rule. Bergmann's rule states that the size of homeothermic organisms increases with latitude; this trend is also common for ectotherms [see e.g., Brown and Lomolino (1998, pp. 488–493)]. Usually, this trend is related to some temperature measure, such as summer maxima or seasonal fluctuations. Food availability increasing with latitude has also been suggested as possible explanation (Kooijman, 2000, pp. 233–234). The model predicts that there is a phenotypical trend showing increasing body size with stronger seasonal food fluctuations. Because food availability often covaries with temperature, our results suggest that organisms become bigger with increasing latitude due to an increasing seasonal variability in food.

The predicted effects of food fluctuations on reproduction are more complex. In a periodically variable food environment, reproduction may increase or decrease with the amplitude of the fluctuations, depending on κ, the parameter characterizing the partitioning of energy between somatic and reproductive tissues. Individuals with a high value for κ commit a relative large fraction of their resources to growth, whereas individuals with a low value for κ give a higher priority to reproduction. High-κ individuals reproduce less with increasing amplitude, but low-κ individuals reproduce more. Although any organism becomes bigger in a periodically variable food environment, and thus feeds at a higher rate, only low-κ individuals translate this extra food intake (partly) into off-spring. High-κ individuals need this extra food intake for maintenance requirements, which also increase with size. Because of the strong size dependence of reproductive output, stochastic variation in the food environment normally leads to enhanced reproduction by individuals that survive the fluctuations. However, in most cases, this increase is accompanied by a still stronger decrease in survival probabilities, causing the expected life time reproduction to decline [see Fig. 9(b)].

The dependency of reproduction patterns on κ in periodic food environments is of particular interest as κ is an adaptive parameter whose value for any particular organism may reflect the intensity of the food fluctuations in a particular environment. The model suggests that a low value for κ would represent a food environment that fluctuates relatively strongly. Also, survival decreases with increasing κ. Thus, individuals in a highly variable food environment are likely to evolve towards a lower κ, a higher reproductive rate and a lower physiological potential for growth than their conspecifics in a less variable food environment. This is in agreement with many data showing increasing clutch sizes in birds and litter sizes in mammals

with increasing lattitude (Brown and Lomolino, 1998). However, the genotypical decrease of growth potential that accompanies a lower value of κ would diminish the above described increase in size due to higher food maxima, causing this trend to be less pronounced.

There are unresolved issues with the rules for partitioning of energy in the model. In general, the parameter κ may be a function of size; for example, the proportion of assimilate assigned to reproduction by the water flea *Daphnia pulex* increases with size (Paloheimo *et al.*, 1982). Recently, it has shown that size dependence in κ is consistent with the other assumptions of his DEB model (Kooijman, 2000), but the effects on dynamics even in a constant environment have not been worked out. Without restrictions on the mathematical form for the size dependence, there is scope for a very wide repertoire of dynamic behavior; further progress would be greatly helped by the development of a mechanistic representation of how an organism's size affects competition for resources between somatic and reproductive tissue.

An equally serious issue is that organisms may change the energy partitioning rules in response to environmental cues that covary with current or anticipated food availability. For example, photoperiod affects reproduction during starvation in the snail *Lymnea stagnalis*; in summer starving animals continue to commit energy to reproduction, but they cut down on this commitment in spring when food tends to be relatively scarce (Zonneveld and Kooijman, 1989). While the precise changes in the expression of the κ-rule are likely to be species specific, an organism that reduces reproduction when there are insufficient resources for growth in a variable environment might be expected to live longer than one that continues to reproduce, since the former organism depletes energy reserves more slowly during periods of starvation.

This observation has led to a variant (here called variant 1) of the κ-rule model, applicable to organisms that cease reproduction when they do not grow (Zonneveld and Kooijman, 1989). We briefly investigated the implications of this modified κ-rule model, though we made a few technical changes to make the model mathematically fully consistent. We also investigated a second variant that allows organisms, which grow and reproduce as in the classic formulation, to utilize all of their reserves before dying of starvation, in contrast to the classic formulation and variant 1, both of which assume that an organism dies when the utilization flux in Fig. 1 is insufficient to meet maintenance costs. With our default parameter set and deterministic food fluctuating with a period of one year, the classic version and variant 1 yield almost indistinguishable growth and reproduction patterns in a periodic food environment. Survival patterns with variant 1 are also similar to the patterns with the classic formulation, which rebuts the intuition articulated above, but is consistent with a previous study of starvation times (Nisbet *et al.*, 1996). In sharp contrast, however, if the organism is able to access all reserves in order to meet maintenance (variant 2), its resistance to starvation is greatly increased, and only in extremely fluctuating food environments does the organism starve to death.

The results from the second variant in the preceding paragraph must be interpreted with considerable caution. The assumptions of the κ-rule model have a strong mechanistic basis and cannot be changed in an *ad hoc* manner without taking care to consider the implications. In particular, the energy utilization flux is derived from assumptions on reserve homeostasis, and an assumption modifying the utilization of energy during starvation must take account of the costs of such a change and should have strong empirical support. Currently, we lack an assumption with these qualities.

We have shown how a variable food environment affects the survival and production of individual organisms that grow in accordance with the κ rule model. A variable food supply stimulates growth, increases mortality and may enhance reproduction, depending on the life history of an organism. More work is needed to investigate the impact of food fluctuations on the evolution of life history parameters and on population dynamics. The work reported in the present paper gives strong guidance on the likely effects on growth and reproduction, and highlights the need for better mechanistic models of mortality.

APPENDIX

In this appendix, we derive the long-term dynamics of the state variables assuming deterministic variation in the environment, in which the scaled functional response fluctuates in a simple periodic fashion. We also show that, in most cases, if an organism is ultimately viable, it can survive the transient periods of starvation that it experienced earlier in life.

The dynamics of the scaled density of energy reserves e and structural biovolume V are given by

$$\frac{de}{dt} = \upsilon V^{-\frac{1}{3}}(t)(f(t) - e(t)), \tag{A1}$$

$$\frac{dV}{dt} = \frac{(\upsilon e(t)V^{\frac{2}{3}}(t) - mgV(t))_+}{e(t) + g}, \tag{A2}$$

where f is the scaled functional response, υ is the energy conductance rate, m is the maintenance rate coefficient, and g is the energy investment ratio.

The dynamics of e are first order and linear in e, and can thus be solved with standard methods, provided that the organism survives to time t. With $e(0)$ being the initial value for $e(t)$, the integral solution reads as

$$e(t) = \exp\left[-\upsilon \int_0^t V^{-1/3}(s)ds\right]$$
$$\left(e(0) + \int_0^t f(t)\upsilon V^{-1/3}(s) \exp\left[\upsilon \int_0^s V^{-1/3}(r)dr\right]ds\right). \tag{A3}$$

Since

$$\upsilon V^{-1/3}(s)\exp\left[\upsilon\int_0^s V^{-1/3}(r)dr\right] = \frac{d(\exp[\upsilon\int_0^s V^{-1/3}(r)dr])}{ds}, \qquad \text{(A4)}$$

equation (A3) is equivalent to

$$e(t) = \exp\left[-\upsilon\int_0^t V^{-1/3}(s)ds\right]\left(e(0) + \int_0^t f(t)d\left(\exp\left[\upsilon\int_0^s V^{-1/3}(r)dr\right]\right)\right). \tag{A5}$$

Integration by parts yields

$$e(t) = f(t) + \exp\left[-\upsilon\int_0^t V^{-1/3}(s)ds\right]$$
$$\left(e(0) - f(0) - \int_0^t f'(s)\exp\left[\upsilon\int_0^s V^{-1/3}(r)dr\right]ds\right). \tag{A6}$$

Further analysis requires a specification of $f(t)$. In particular, we are interested in the consequences of a sinusoidally fluctuating scaled food density with angular frequency ω, amplitude a and mean value f_a. The second integral in equation (A6), $A \equiv \int_0^t f'(s)\exp\left[\upsilon\int_0^s V^{-1/3}(r)dr\right]ds$, can now be evaluated:

$$A = a\omega\int_0^t \cos(\omega s)\exp\left[\upsilon\int_0^s V^{-1/3}(r)dr\right]ds$$

$$= \frac{a\omega}{2}\int_0^t (\exp[\iota\omega t] + \exp[-\iota\omega t])\exp\left[\upsilon\int_0^s V^{-1/3}(r)dr\right]$$

$$= \frac{a\omega}{2}\left(\int_0^t \exp\left[\int_0^s (\iota\omega + \upsilon V^{-1/3}(r))dr\right]ds\right.$$

$$\left. + \int_0^t \exp\left[\int_0^s (-\iota\omega + \upsilon V^{-1/3}(r))dr\right]ds\right)$$

$$= \frac{a\omega}{2}\left(\left[\frac{\exp[\int_0^s(\iota\omega + \upsilon V^{-1/3}(r))dr]}{\iota\omega + \upsilon V^{-1/3}(s)}\right]_0^t + \left[\frac{\exp[\int_0^s(\iota\omega + \upsilon V^{-1/3}(r))dr]}{-\iota\omega + \upsilon V^{-1/3}(s)}\right]_0^t\right).$$

After some tedious algebra we get

$$A = a\omega\left(\frac{-\upsilon V_b^{-1/3}}{\omega^2 + (\upsilon V_b^{-1/3})^2} + \exp\left[\upsilon\int_0^t V^{-1/3}(s)ds\right]\right.$$

$$\left.\left(\frac{\omega\sin\omega t + \upsilon V^{-1/3}(t)\cos\omega t}{\omega^2 + (\upsilon V^{-1/3}(t))^2}\right)\right), \tag{A7}$$

in which $V_b \equiv V(0)$ is the structural body volume at birth. Substituting this result back into equation (A6) yields

$$
e(t) = f_a + \left(e(0) - f_a + \frac{a\omega\upsilon V_b^{-1/3}}{\omega^2 + \upsilon^2 V_b^{-2/3}} \right) \exp\left[-\upsilon \int_0^t V^{-1/3}(s)\,ds \right]
$$
$$
+ \frac{a}{1 + \left(\frac{\omega V^{1/3}(t)}{\upsilon} \right)^2} \left(\sin\omega t - \frac{\omega V^{1/3}(t)}{\upsilon} \cos\omega t \right). \tag{A8}
$$

We are now able to determine the long-term dynamics of e and V. Because υ and V are positive and bounded above, the middle term in equation (A8) fades with time, and since $V^{1/3}$ is a non-decreasing function of time, the other two terms represent a sinusoid with a non-increasing amplitude (and non-decreasing period). The highest scaled energy density in a cycle of this sinusoid, $e_{\max}$, decreases as the organism grows. This implies that growth eventually ceases, since V is bounded through e [see equation (A2)]. An organism will continue to grow provided $V^{1/3} \leq e_{\max}\upsilon/mg$, and has a maximum volumetric length given by $\bar{V}^{1/3} = e_{\max}^*\upsilon/mg$ for some $e_{\max}^*$. Now assume some cycle n in which the organism reaches its maximum volumetric length supported by that cycle, $V_n^{1/3}$; then $V_n^{1/3} = e_{\max}(n)\upsilon/mg$. If the organism continues to grow in some later cycle o, then we must have $e_{\max}(o) > e_{\max}(n)$. But we already know that $e_{\max}(o) \leq e_{\max}(n)$. Hence, growth is bounded, implying that the dynamics of e will approach the limit cycle

$$
\bar{e}(t) = f_a + \frac{a}{\sqrt{1 + \left(\frac{\omega \bar{V}^{1/3}}{\upsilon} \right)^2}} \sin(\omega t + \phi), \tag{A9}
$$

where $\phi = \tan^{-1} \frac{\omega \bar{V}^{1/3}}{\upsilon}$ is a measure (in radians) of the extent to which fluctuations in e ultimately lag behind f. Then, $e_{\max}^* = \bar{e}_{\max}$ the highest scaled energy density in the limit cycle, and $\bar{V}^{1/3} = \bar{e}_{\max}\upsilon/mg$.

It is highly likely that if an organism is able to survive the limit cycle, it is also able to survive the transient. It is sufficient to assume that $e(0)$ lies within the range of possible values for $f(t)$, which is true in the κ-rule model, for instance, when off-spring experiences a food environment similar to that of the mother (the model assumes that hatchlings have the same energy density as the mother at the time of egg laying). The model assumes that an organism is viable when the energy mobilized from the reserves is sufficient to meet somatic maintenance demands, that is, when

$$
V^{1/3}(t) \leq \frac{e(t)\upsilon}{\kappa mg}, \tag{A10}
$$

in which κ is the parameter partitioning reserves between somatic and reproductive tissues. With $V_m^{1/3} = \upsilon/mg$, the maximum volumetric length an organism can

attain, equation (A10) implies that death is inevitable when $e(t) = \frac{\kappa V^{1/3}(t)}{V_m^{1/3}}$ while $\frac{de}{dt} \leq 0$, that is, while $V^{1/3}(t) > \frac{f(t)V_m^{1/3}}{\kappa}$ [see equation (A1)]. Because $\kappa \in (0, 1]$ and $f(t) \leq f_a + a \equiv f_{\max}$, an organism is nonviable when $V^{1/3}(t) > f_{\max} V_m^{1/3}$. But with a periodically variable scaled food density $V^{1/3}(t) \leq \bar{V}^{1/3} = \bar{e}_{\max} V_m^{1/3} < f_{\max} V_m^{1/3}$. Hence, organisms that are viable in the limit cycle, are also viable during transient dynamics.

ACKNOWLEDGEMENTS

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